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## THE EVOLUTION OF COMMUNICATION

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### **The ethological approach to communication**

One of the most important methodological contributions of ethology to the behavioral sciences has been the recognition that behavior can be studied at different levels of analysis, and in particular at the levels of ontogeny, causation, function, and evolution (Tinbergen, 1963). Ontogeny refers to the developmental changes of behavior over the lifetime of an individual. Causation refers to the mechanisms and stimuli—external and internal—that control and regulate behavior. Function encompasses both the immediate consequence or function of behavior and its adaptive value for the survival and reproductive success of the individual. Finally, evolution refers to the origin and modification of behavior in relation to the processes of speciation and adaptive radiation. Researchers often focus on one aspect of behavior independently from all the others, but a full understanding of behavior requires an integration of different levels of analysis.

Recognizing that every behavioral phenomenon needs at least four different types of explanations requires some training. Behavioral scientists who are not familiar with ethology often ignore the evolutionary level of analysis and sometimes fail to recognize the differences between the causal and functional explanations of behavior. In fact, behind some controversies in the behavioral sciences there is often miscommunication between scientists investigating different aspects of the same phenomenon. The contrast between Ekman and Fridlund over the interpretation of human facial expression (see Ekman, 1994; Fridlund, 1994) is a potential case in point. Ekman's contention that facial expressions mostly reflect underlying emotional states is derived from an interest in the proximate causation of the phenomenon, whereas Fridlund's view of expressions as social signals used to mediate and manipulate social interactions reflects an emphasis on the function.

Communication, just like any other behavioral phenomenon can be studied at the ontogenetic, causal, functional, and evolutionary level. The study of animal communication is a vast and rapidly advancing research field and most scientists specialize in one level of analysis (e.g. causal) of one type of communicative interaction (e.g. mating-related) in one communication modality (e.g. auditory) of one species (e.g. the squirrel monkey). As a consequence of this extreme specialization, researchers interested, for example, in the neural control of mating vocalizations in a certain species usually know little about the effect of rate of vocalizations on the individual's mating success, or if and why a closely-related species uses different vocalizations. To further complicate matters, some researchers study communication as a vehicle to understand the social behavior and ecological

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adaptations of a certain animal species, whereas others are interested in communication only as window into the cognitive and linguistic abilities of animals relative to humans. Thus while the former are interested in variability among species, individuals and environments, the latter usually focus on one species and one environment in the attempt to gain knowledge of mechanisms and principles that have general validity and that can be directly related to humans.

When we move from animal communication to human language, the number and the heterogeneity of the possible research approaches to the subject is such that we even find it difficult to agree on a definition of language. For example, the evolution of language is a subject of study which could be easily approached by a variety of different disciplines including anatomy, anthropology, archeology, biology, linguistics, mathematics, physics, and psychology, each with its own numerous sub-specialties.

The boundaries between different disciplines, of course, like those between different levels of analysis, do not correspond to objective demarcations of the external reality but are just a heuristic device to make the work of scientists more manageable and improve the focus of their research. To fully understand phenomena as complex and multi-faceted as communication and language, the boundaries between different levels of analysis and different disciplines must be repeatedly crossed and information exchanged and integrated.

### **The study of communication: a new synthesis**

In writing his book *The Evolution of Communication* (1996), Marc Hauser deserves credit for having attempted the formidable task of reviewing the research on communication and language. The title of the book is somewhat misleading because it suggests that the author has taken only one of the many possible approaches to the subject. In reality, Hauser has attempted to synthesize the literature on communication exploring all the four Tinbergenian levels of analysis and repeatedly crossing the boundaries between different disciplines and those between animal communication and human language. The book is the result of a massive effort, with over 750 pages crammed with research findings, graphs, tables, and references. After a few introductory chapters that set the historical and conceptual background for the study of communication and language, the bulk of the book is organized into four major sections. Two of them focus on proximate mechanisms—neurobiological and psychological—underlying animal and human communication. One section focuses on ontogeny and one on adaptive function. The final chapter sums up a few of the major themes of the book and provides some directions for future research.

Marc Hauser deserves credit not just for attempting the enterprise of writing a book on communication but also for being successful at it. *The Evolution of Communication* is more than a careful and up-to-date review of research findings. In almost every topic treated in the book, Hauser offers a personal perspective, a conceptual or methodological contribution, or an attempt at integrating the findings of different studies and reconciling opposite views. His style is lucid and entertaining and carries the reader through even somewhat dull sections of the book, those with sound spectrograms on almost every page.

Despite its considerable size, *The Evolution of Communication* is not a comprehensive synthesis of our knowledge of communication (and how could it be?); with the material that was left out one could write one (or more) volume(s) of the same size as Hauser's. Hauser explicitly restricted his synthesis to communication in the auditory and visual

modalities to the dismay of all the animals who communicate with their nose, the scientists who study them, and all of us who enjoyed reading *Perfume* (Süskind, 1985). Within the area of auditory and visual communication, he made a less explicit but equally drastic selection of topics, presumably on the basis of his own interests and biases, as well as those of the contemporary scientific community. Even readers who are not familiar with Hauser's own main area of research (primate vocalizations) will easily notice that he is more comfortable discussing vocal and verbal communication than visual signals, and that his interests lean more towards the analysis of causation and ontogeny than towards that of function and evolution.

Perhaps it is no surprise that Hauser's most valuable contributions in *The Evolution of Communication* are in the critical evaluation of the research in his own area of expertise. In one of the last sections of the book, he offers a sound and honest assessment of the pros and cons of playback experiments with monkey vocalizations and provides some specific indications for the design and implementation of future experiments in this area. He also has some interesting suggestions about the conceptualization of animal signals but his ideas needed to be further developed. For example, in the initial chapter, a distinction is drawn between signals, cues, and signs. In Hauser's view, signals such as vocalizations and facial expressions have been designed by natural or sexual selection to be informative in response to pressures from the environment, they are costly to produce (e.g. in terms of energy expenditure or increased exposure to predators), and they can be turned ON and OFF (i.e. they occur only in specific circumstances). Cues, like signals, represent potential sources of information, but they correspond to permanent features of an individual's or species' phenotype and their expression carries no extra cost (e.g. the sexual ornaments of some birds or the warning colors of some poisonous snakes). Unlike signals and cues, signs provide information to perceivers regarding the characteristics and activity of the individual, but they have not been designed to be informative in this specific way. Examples of signs are the tracks left by lions or snakes. Hauser acknowledges that there may be exceptions to this generalization and that the use of this classification may sometimes be equivocal. For example, the mating call of a male frog should be classified as a signal if perceived by a female frog of the same species, but as a sign if perceived by a predator. Perhaps because of this problem, after a promising appearance in the first pages of the book, the distinction between signals, cues, and signs is mentioned only a couple of times, and in only one case is the heuristic value of such a distinction clearly demonstrated.

Other problems of definition arise when Hauser discusses the information content of animal signals. As he points out, there has been an amazing proliferation of terms to describe whether signals are associated with the signaler's affective or external state. In relation to affective state, we speak of emotional, affective, and motivational signals, whereas for external state the signals may be referred to as semantic, referential, representational, indexical, or symbolic. Hauser thinks that it is important to draw a line between signals that reflect emotional and motivational states and signals that are referential and representational. Then he proceeds to give directions on to how to classify the signals into these different categories. For example, he writes that signals (at this point we must keep in mind that by signals he really means vocalizations) are emotional when they are associated with an underlying emotional state. So far so good. But how do we know if vocalizations are associated with an emotional state, and what state they are associated with? Hauser's answer is that we infer the emotional state from nonacoustic signals (facial expressions or body postures) or the context in which the signal occurs. In other words,

here and throughout the book, Hauser assumes that facial expressions and other nonvocal signals necessarily reflect emotion and that their main utility is in telling us whether or not the accompanying vocalization should be classified as emotional. I find this view particularly striking because I am often inclined to classify facial expressions as emotional or nonemotional depending on whether or not they are accompanied by vocalizations (e.g. screams) rather than the other way around.

After taking care of the definition of emotional and motivational signals, Hauser draws the following distinction between semantic, representational, and referential signals. Signals are semantic if they provide listeners with information about objects and events in the environment. Signals are representational if listeners create some kind of mental picture of the object or event eliciting the signal, and they are referential if they are reliably associated with objects and events in the world. The considerable degree of overlap between the definitions of semantic, representational, and referential signals (e.g. semantic and referential are almost the same, and both seem to be included into the definition of representational), however, raises some doubts about the heuristic value of such a distinction and confirms my impression that definitions are not one of the major strengths of Hauser's book.

Despite the unquestionable value of the book as a resource for both research and teaching, *The Evolution of Communication* is bound to upset many of its readers. Since the book is presented as a comprehensive synthesis of the research on communication, those scientists whose area of expertise was not included in the synthesis will feel that their work has been dismissed. Moreover, like other previous attempts at multi-disciplinary synthesis, the book will arouse some suspicion in those scientists who have a territorial view of their own area of specialty, and who are often wary of attempts at trespassing from other territories. I suspect that territorial displays involving hair-raising, vocalizations, and (why not?) also olfactory signals, will be especially likely on both sides of the fence separating animal communication and human language, which Hauser purposefully and repeatedly crosses in his book without much circumspection.

I probably belong to a minority of readers who are somewhat upset about the title of Hauser's book for creating an expectation that was not fulfilled. What I found missing in *The Evolution of Communication* is a systematic and comprehensive analysis of communication at the evolutionary level, the fourth in Tinbergen's distinction. Hauser does acknowledge the importance of studying evolutionary trends in communication systems and linguistic abilities across different animal taxa in the introductory and conclusive chapters of the book. He even argues that 'by focusing on taxonomic groups that use either auditory or visual signals, we open the opportunity to explore homologous as well as homoplastic traits for a substantial set of species' (p. 5). The evolutionary analysis, however, and in particular the exploration of homologies, occupies a marginal role in the book relative, for example, to the neurobiological and cognitive bases of communication and language.

The evolutionary study of communication received great emphasis by European ethologists in the first part of this century, and some classical ethological studies—unfortunately overlooked by Hauser—focused on the phylogeny of visual signals in several species of birds (Heinroth, 1911; Lorenz, 1941; Hinde, 1955; Andrew, 1956; Tinbergen, 1959, 1962) and fish (Baerends and Baerends, 1950). For example, stimulated by studies conducted by Heinroth and Lorenz (1941) on the courtship displays of ducks (*Anatidae*), Tinbergen launched a large-scale study of numerous species of gulls to investigate the

causation, function, and origin of visual displays 'with the ultimate aim of understanding how they could have originated and diverged in the course of speciation' (Tinbergen, 1959). Tinbergen's work with gulls identified considerable intraspecific and interspecific variability in the morphology of several courtship and agonistic displays and led to a classification of this variability into four distinct categories, each resulting from a different selective pressure: 1) interspecific differences due to selection pressures acting on each display separately; 2) intraspecific differences due to selection towards interdisplay distinctness; 3) interspecific differences directly selected for; and 4) interspecific differences developed as a consequence of pressure promoting differences in other functional systems. The evolutionary approach undertaken by Tinbergen allowed him to confirm the hypothesis advanced by taxonomists that gulls are a monophyletic group as well as to trace the most probable evolution and modification of displays within the group.

Unfortunately, the evolutionary approach exemplified by Tinbergen's research with gulls has traditionally been the least popular contribution of European ethology in the U.S. Nowadays, the evolutionary road is the least traveled of all four by the communication and language researchers, especially in the American continent (I suspect that if *The Evolution of Communication* had been written in Oxford, U.K., instead of Cambridge, MA, it would have been a very different book). Although it is true that the publication of Dawkins and Krebs's (1978) seminal paper on manipulation in animal signals brought about a considerable revision of ethology's view of the evolution of communication, the massive amount of information gathered by ethological studies conducted in the 1940s through the 1960s should not be thrown away with the bathwater.

The failure to review some classical articles on the phylogeny of bird displays is a relatively minor evil of *The Evolution of Communication*, because it will probably go unnoticed by many of its readers. More importantly, I feel that Hauser missed a good opportunity to address some important evolutionary questions about communication and language that would have nicely complemented his multi-levelled and multi-disciplinary synthesis. In the rest of this article, I would like to sketch some of the themes that could perhaps be developed in one of the next volumes of *The Evolution of Communication*.

### **The evolution of communication and the comparative method**

From a functional and evolutionary perspective, communication is a social adaptation. As long as the survival and reproduction of a living organism is affected by the presence and activity of other living organisms of the same or of a different species, the ability to exchange information between these organisms will be selected for by natural or sexual selection. In the living world, there is enormous variability in how organisms communicate with each other and in what they communicate to each other. This variability is determined by the type of social environment in which they live and by the constraints imposed by the physical environment, the organisms' own biological characteristics, and their phylogenetic history (see below). In my view, an evolutionary approach to communication would mainly involve identifying the selective pressures and the constraints that are responsible for differences in how organisms communicate and in what they communicate to each other.

Communication is almost always a process involving multiple sensory modalities. However, there is variability among species in which communicative channels are prominent over the others. From an evolutionary perspective, it would be important to identify the relative role played by each channel (e.g. visual versus vocal, versus tactile, etc.) in the

communicative repertoire of different species and identify the selective pressures and the constraints (biological, ecological, and phylogenetic) that account for such variability.

Understanding what organisms communicate to each other is as important as understanding how they communicate. In some animal species, individuals communicate with their conspecifics mainly about the location of food sources, whereas in others they mainly communicate about predator detection, or social interactions such as aggression, affiliation, or mating. Even in the same contexts of communication, some species have much wider repertoires of signals than others. From an evolutionary perspective, it would be important to identify the selective pressures and the constraints responsible for differences in the contextual usage of signals and in the size of the signal repertoires in different species.

Ethologists have traditionally attempted to address some of the above-outlined issues with the comparative method, namely by comparing closely-related species living in different social and ecological environments (Lorenz, 1958; Tinbergen, 1953, 1962). In its most popular version, the comparative method involves making comparisons across taxa in order to identify associations between traits or between traits and environments that might suggest adaptive explanations of trait function. For example, the correlation between the prominence of vocal signals and an arboreal lifestyle and that between visual signals and terrestriality across a number of primate species would suggest that vocalizations are an adaptation to living conditions with poor visibility (Marler, 1965). The comparative method, however, can also be used to provide information concerning the historical origin of the trait and the sequence and direction of its evolutionary transformations. For example, the comparison of the structure and contextual usage of facial expressions in humans and nonhuman primates suggests that the human smile is an evolutionary derivation of the bared-teeth display observed in a variety of monkeys and apes (van Hooff, 1972).

Both uses of the comparative method are partly right and both are less than the whole story (Harvey and Pagel, 1991). Although it is true that distantly-related species living in similar environments could evolve similar patterns of communication, it is also true that a form of communication is not exactly like a ball of clay that lies ready to take on any shape the outside forces impose upon it. It is important, therefore, that comparative analyses investigating the adaptive significance of communicative patterns be conducted from an historical perspective (Wenzel, 1992; Miles and Dunham, 1993).

Ultimately, the goal of a comparative analysis of communication across different animal taxa is to understand the type of changes that have occurred in the evolution of communicative systems and be able to predict the communication system of a species (e.g. the type, structure, and number of signals used) based on the knowledge of its social system, ecological environment, and biological constraints. This would be particularly valuable for extinct species such as those of the hominid line, for which we can obtain some of the relevant information from the archeological record.

*The Evolution of Communication* clearly shows that the study of the communicative abilities of our closest relatives, chimpanzees and bonobos, but also of macaques, birds, and frogs—just to cite some of Hauser's favorite animals—at the levels of mechanisms (neurobiological and cognitive), ontogeny, and function can help us understand why and how humans communicate the way they do. However, a comparative and evolutionary analysis of communication systems across different taxa, and in particular across all the Primates, the Mammals, and the Vertebrates, could make an important contribution to our understanding of the evolution of human language as well.

### The evolution of language

The evolutionary history of human language is a history in which random and opportunistic events probably played an important role, just like in any other evolutionary history. However, it is probably also a history with no miracles, just like any other human or animal history (Wilcox, 1996). Unless we possess enough information to reconstruct the evolutionary changes in the vocal tract and brain structure step by step along the hominid line, understanding exactly *how* language evolved, whether from primate vocalizations and gestures or from some pre-existing noncommunicative faculty, is a question that we may never be able to answer. This is because, in evolution, the same outcome can often be reached through different paths so that, for example, the same language could evolve from primate communication on this planet and from something else on a twin planet in a different solar system. Viewing language, however, as a form of communication adapted to the social environment may allow us to understand *why* language evolved and explain some of its peculiar characteristics.

The use of comparative studies of communication to investigate the evolution of language is today advocated by a number of biologists, including Hauser, as well as anthropologists (see King, 1994), but is met with resistance by those linguists who regard language as more than a form of communication. In particular, linguists of the Chomskian school view language as a formal symbolic structure composed of many parts: syntax, with its discrete combinatorial system building phrase structure; morphology, a second combinatorial system building words; lexicon; phonological rules and structures; speech perception, and parsing and learning algorithms (Pinker, 1994). Much of Chomsky's research effort has gone into dissecting and describing the formal properties of language (e.g. Chomsky, 1957) and questions of ontogeny, causation, function, and evolution have occupied a relatively marginal role in this type of work. For example, Chomsky's view that language development is instinctive, that language is the product of an unspecified language organ in the brain, and that language originated from structural properties of the brain that developed for other reasons (but see Pinker and Bloom, 1990) sounds more like an acknowledgement of ignorance and lack of interest in further pursuing the analysis than the inescapable conclusion of a systematic research program.

When it comes to deciding whether or not comparative studies of communication can be useful to understand the evolution of language, the functional significance of language and its components (syntax, grammar, lexicon, etc.) becomes a crucial question. Three hypotheses concerning the function of language at the time of its origins have been postulated; first, that language had no adaptive function at all and was merely a by-product of certain brain structures developed for other purposes; second, that language served social purposes, namely had a communicative function; and third, that language developed as a cognitive tool that improved our ability to think about and understand the world.

The first hypothesis, although as plausible as the others, has little heuristic value from a research standpoint. Almost any trait in the course of evolution might have resulted by chance or as a by-product of another trait but we would not be able to prove it. In contrast, we could deduce the probability that language was the product of selection by showing that possession of language would be favored by selection. Moreover, testing adaptive hypotheses invariably promotes a great deal of research and knowledge. In fact, the heuristic value of the adaptationist approach is one of the reasons why we should first attempt to explain biological phenomena and processes as the product of natural selection, and only after all attempts have failed, resort to non-adaptationist explanations (Mayr, 1983).

As far as the adaptive function of language is concerned, I tend to side with the view that the selective advantages of language are to be found in the social sphere of human life. In fact, I cannot escape the impression that theories of language origins emphasizing its cognitive significance reflect a view of the world from the top of academic ivory towers. Although there is no question that some of the most uncanny peculiarities of human language are found in its formal properties and in the cognitive domain, I am under the impression that most people living at the bottom of the ivory towers do not use language for talking to themselves but to communicate with other people. In fact, analyses of language use and conversation contents in pre-urban and modern societies have shown that language is mostly used for establishing, maintaining, and refining social relationships (Burling, 1986; Dunbar, 1993).

The fact that language is nowadays mostly used for communicative/social purposes, of course, does not imply that this is the function for which language was selected at the time of its origins. In other words, language could have been selected for because of its cognitive significance and have subsequently acquired a communicative function. If this were true, then it would be more useful to investigate the evolutionary antecedents of language among the cognitive abilities of nonhuman animals or hominids rather than their communication systems. The assumption that the current function of a trait is also the function that was selected for when the trait evolved, however, is often the most parsimonious approach to be used when making inferences about the past. Since science is guided by parsimony, if I had to investigate the origins of language and place all of my intellectual and research resources on the safest bet, I think that I would do what Hauser recommends and set out to study the evolution of communication.

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## REFERENCES

- Andrew, R. J. (1956) The aggressive and courtship behaviour of certain *Emberizinae*. *Behaviour* **10**, 255–308.
- Baerends, G. P. and Baerends, J. M. (1950) An introduction to the ethology of cichlid fishes. *Behaviour* (Suppl.) **1**, 1–242.
- Burling, R. (1986) The selective advantage of complex language. *Ethology & Sociobiology* **1**, 1–16.
- Chomsky, N. (1957) *Syntactic Structures*. Mouton, The Hague.
- Dawkins, R. and Krebs, J. R. (1978) Animal signals: information or manipulation? In *Behavioral Ecology*, eds J. R. Krebs and N. B. Davies, pp. 289–309. Blackwell Scientific Publications, Oxford.
- Dunbar, R. I. M. (1993) Coevolution of neocortical size, group size and language in humans. *Behavioral and Brain Sciences* **16**, 681–735.
- Ekman, P. (1994) Strong evidence for universals in facial expressions: a reply to Russell's mistaken critique. *Psychological Bulletin* **115**, 268–287.
- Fridlund, A. J. (1994) *Human Facial Expression. An Evolutionary View*. Academic Press, New York.
- Harvey, P.H. and Pagel, M. D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- Hauser, M. (1996) *The Evolution of Communication*. MIT Press, Cambridge, MA.

- Heinroth, O. (1911) Beiträge zur Biologie, namentlich Ethologie und Psychologie der Anatiden. *Proceedings of the 5th International Ornithological Congress*, Berlin 1910, pp. 589–702.
- Hinde, R. A. (1955) A comparative study of the courtship of certain finches. *Ibis* **97**, 706–745.
- King, B. J. (1994). *The Information Continuum. Evolution of Social Information Transfer in Monkeys, Apes, and Hominids*. School of American Research, Santa Fe, NM.
- Lorenz, K. (1941) Vergleichende Bewegungsstudien an Anatinen. *Journal of Ornithology* **89**, 194–294.
- Lorenz, K. (1958) The evolution of behavior. *Scientific American* **199**, 67–78.
- Marler, P. (1965). Communication in monkeys and apes. In *Primate Behavior: Field Studies of Monkeys and Apes*, ed. I. De Vore, pp. 544–584. Holt, Rinehart and Winston, New York.
- Mayr, E. (1983) How to carry out the adaptationist program? *American Naturalist* **121**, 324–334.
- Miles, D. B. and Dunham, A. E. (1993) Historical perspectives in ecology and evolutionary biology. *Annual Reviews of Ecology and Systematics* **24**, 587–619.
- Pinker, S. (1994) *The Language Instinct*. William Morrow & Co, New York.
- Pinker, S. and Bloom, P. (1990) Natural language and natural selection. *Behavioral and Brain Sciences* **13**, 707–784.
- Süskind, P. (1985) *Perfume*. Washington Square Press, New York.
- Tinbergen, N. (1953) *Social Behavior in Animals*. Chapman & Hall. New York.
- Tinbergen, N. (1959) Comparative studies of the behaviour of gulls (*Laridae*); a progress report. *Behaviour* **15**, 1–70.
- Tinbergen, N. (1962) The evolution of animal communication—A critical examination of methods. *Symposia of the Zoological Society of London* **8**, 1–6.
- Tinbergen, N. (1963) On the aims and methods of ethology. *Zeitschrift für Tierpsychologie* **20**, 410–433.
- van Hooff, J. A. R. A. M. (1972). A comparative approach to the phylogeny of laughter and smiling. In *Non-Verbal Communication*, ed. R. A. Hind, pp. 209–241. Cambridge University Press, Cambridge.
- Wenzel, J. W. (1992) Behavioral homology and phylogeny. *Annual Reviews of Ecology and Systematics* **23**, 361–381.
- Wilcox, S. (1996) Not from Jove's brow. *Language & Communication* **16**, 179–192.